# Diversity and Stability: A Practical Proposal and a Model of Interdependence

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## INTRODUCTION

*Diversity* and *stability* are commonly used in ecology to express aspects of "organization" of ecosystems. They must be measurable. Diversity, related to the distribution of the present biomass, to its complexity at a given time, may have achieved this desirable status, but much ambiguity remains concerning definition and measurement of stability. The purpose of this paper is to try to find what is behind "stability," when the word is used in an ecological context, and to find some way to measure it. The strongest motivation for such an attempt is that diversity is insufficient as a measure of organization and needs to be complemented by some expression of persistence in time, or order.[1,2] It is a matter of choice, and may be confusing, to apply the word *stability* to this quality of persistence. Perhaps it will turn out that the function that I propose has no relation to what others understand by stability. This makes even more necessary an explanation of what is meant by diversity and stability. Any empirical approach requires that both functions be computed on independently measured parameters.

Another purpose of this paper is to try to link all major "macroscopic" or synthetic properties of an ecosystem, including especially production, biomass, diversity, and stability, in a single expression. At its present stage, such an expression cannot be much more, and could be less, than shorthand for ecological reasoning, not yet fit to be fed into computers. If the general form of the expression survives criticism, we must then think about its definitive form, including constants and units.

## DIVERSITY

In ecology the notion of diversity has its roots in consideration of the richness and variety of species in a community, but the concept of diversity can be applied to the distribution of the elements of any set in subsets, e.g., the individuals of a unispecific population distributed in year classes; particles counted in size classes; the components of a chemical mixture counted in molecules of different kinds. Diversity is obviously dependent on our decision or on our capacity to discriminate: the individuals of an ecosystem can be classified as to species, as to genotypes, or even as to kinds of DNA.

Diversity can be expressed by any monotonous function having a minimum when all the elements present belong to the same class and a maximum when every one of the elements belongs to a different class. The function is selected on the basis of expediency, and it should be almost invariant to the usual accidents in the

sampling and treatment of data. For instance, the function should be relatively insensitive to the size of the sample, embodying the usual pattern of distribution of individuals in species; it should also be insensitive to any random selection within the sample, and, if possible, to operations that are not strictly random, such as those dependent on the method of sampling and on the taxonomic groups selected for study. Taxonomic groups that cover a broad ecological spectrum – as Chydoridae do in freshwater lakes – are in a good position to give an estimate of the distribution of overall diversities, with all their implications. Other groups ecologically more specialized, such as the diatoms in the marine plankton, are less appropriate.

The usual function of Shannon-Weaver is acceptable with respect to the points mentioned. The factorial expression, basically equivalent, is intuitively more appealing to the biologist, as it represents diversity as proportional to the number of relations that can be established among the elements of a set, and this may have some bearing on the number of actual feedback circuits effective in the system.

Regularity in the distribution of individuals into species fascinated the first students of diversity. It is a consequence of the fact that the classes into which the individuals fall are linked by definite relations. The simplest example is offered by the age classes in a unispecific population: if mortality is constant, stable distribution follows the law of geometric progression; but if there is an acceleration in the addition of juveniles, diversity drops. Similarly, the interactions within the ecosystem generate and alter the quantitative relations between the numbers of individuals of the different species. Although diversity appears as an instantaneous property, it results from the function of the ecosystem.

The preferred expression for diversity is a statistical function that implies no particular regularity in distribution, and in whose computation the numbers of individuals in all the species are taken into account. Such an expression is not immune to the sort of criticism that has been leveled at other expressions based on definite statistical or deterministic hypotheses about the regular distribution of individuals into species. Perhaps the most critical aspect of all the methods of computing and treating diversity is the dependence on size of sample. The relations between diversity and space make it necessary to work with spectra of diversity which imply a hierarchy of structures that has led to the recognition and separation of simple diversity at a low level and pattern diversity.[3] As the example presented in Figure 1 shows, it is possible to have the same value of diversity for a given sample size within structures that are completely different. As will be deduced later, the form of the spectrum appears to be related to the persistence (or stability).

Diversity, measured as usual in bits per individual, reaches its upper limit at around 5. This, $K$, is a "universal constant" in organization. Perhaps this is a consequence of limitations of a topological nature in the possibility of having interaction or meaningful relations between elements of a structure. A practical consequence is that the scale offered by diversity as a measure of the complexity of an ecosystem is rather limited. If it is necessary or desirable to enlarge it, spectra of diversity must be used, or some further measurement such as persistence must be introduced.

The concept of diversity as used in ecology, as an expression of a particular distribution of individuals into species, does not necessarily have any implications concerning information and thermodynamics. Nevertheless it may be interesting to consider how diversity can be formulated in terms of information theory. We may assume that in a very diverse community we approach every individual with more

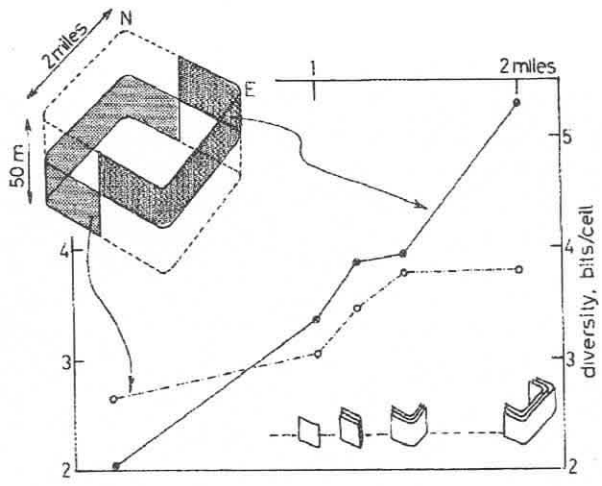


Figure 1. Averaged diversity for phytoplankton populations pooled over spaces of increasing size, in two neighboring segments of a square intensely sampled in the western Mediterranean, July 1968. The populations in the inferior NW section were rich in diatoms, actively multiplying in mixed water, and diversity was very high at the lowest end of the spectrum. Populations in the upper SE section were rich in dinoflagellates, and they gave a "normal" spectrum of diversity.

uncertainty in what concerns its identity and thus every individual carries a higher amount of information; it can be said that a more diverse community carries more information. In such a community, a larger sample is necessary to have an estimate of the representation of every one of the species.

A more diverse system, once studied, is usually also a more predictable system. As it is possible to say that accumulated and assimilated information allows the system to anticipate environmental change, it is tempting – but may be misleading – to see here a way to equate diversity and information. The problem is how to deduce organization, in the sense of richness of actual interactions between elements, from diversity. Although in nature more diverse systems are often also more stable, as most biologists would accept, the relationship comes from historical circumstances, and in the context of information theory the independence of the two properties is apparent. Diversity ($D$) is a measure of the width of the communication channel;[1] at any moment the asset of an ecosystem is a number of species represented by given numbers of individuals. But the predictability depends on how this assemblage works, it may be a well organized community able to sustain itself indefinitely in a given environment, or a haphazard assemblage of drifters. It seems necessary to add a measure of the stability or persistence ($S$) equal to the inverse of the deterioration of information during its transmission. This is analogous to "noise." The effective capacity of the channel can be written as approximating the difference, $D-(1/S)$.

$D$ is diversity, computed through the usual Shannon-Weaver function, $D=-p_i \log_2 p_i$, expressed in bits per individual. $D$ has no dimensions. $S$ will be defined later; it is infinite if no element of the system experiences a loss or a change and zero if every element is lost or changed in an unpredictable way in every unit or compartment of time. The dimension of $(1/S)$ is time, but some other form $(c/S)$ can be proposed if dimensional consistency so requires.

## STABILITY

In everyday terms a system is stable if, when changed from a steady state, it develops forces that tend to restore it to its original condition. Several authors[4-6] have stressed the imprecision of the concepts of stability and regulation. Ashby[5] comments that the notion of stability includes something linked to the fact that, although a system is passing through a series of changes, some aspect of it is unchanging: a statement about general conditions that the interactions fulfill may be a statement concerning the stability. A set of states that are interconvertible, but generate no new states, is another element to be included in the notion of stability; as well as the existence, around this set of states, of another set to which the system does not go spontaneously, but if led to it can return to the interior first set. If the system is led outside the exterior set, no prediction is possible. This can be represented graphically as in Figure 2, left. A matrix can be the appropriate practical representation, and in cybernetic terms the system has feedback circuits in which the negative (or stabilizing) ones predominate.

An appropriate starting point in discussing the concept of stability is to write in the usual form the interactions between the elements of an ecosystem:

$$| dN_i/dt = e_i N_i + \sum^{j} a_{ij} N_i N_j | \quad i = 1, 2, \ldots . n .$$

To the degree that an ecosystem is described by such a matrix, it can reach a stationary state. The outputs are the changes in numbers of the different species (the set of $dN_i/dt$), and they act as inputs for a new cycle, until the system arrives at a situation that is either stationary or has regular rhythms (Figure 2, right). This model is equivalent to the core $A$ of Figure 2, left. Changes not accounted for (changes in the environment, immigration or emigration) can lead the system to the peripheral field ($B$), but the changes can eventually be assimilated or buffered by the play of the same input-output matrix. Perhaps some changes will result in a structure so different from the initial one that the convenience of continuing to call it the *same* ecosystem can be challenged; nevertheless the mechanism of building up complexity works as always, and at least this fundamental property of the ecosystem is preserved.

If stability is to be a useful concept, it needs quantification, but the difficulties appear forbidding. A matrix like the ideal one, but with reference to a concrete ecosystem, has never been specified. Suppose this could be done. One might choose as an expression of stability the ratio between the size of the whole area of the states from which the system can return and where it goes under the impact of moderate environmental disturbance, including such changes as massive migration, and the size of the area covering the set of spontaneously interconvertible states in which are included the results of adjustment to or anticipation of predictable environmental change, as well as cycles generated by interaction between species. This would amount to the ratio between the area $B$ and the area $A$ in Figure 2. Stability would be zero if area $B$ is null. But this is not a reliable solution, since both areas under consideration are probably always more or less related; that is, systems that spontaneously fluctuate more can also return from a wider range of induced deviations. Moreover, the boundary between the two areas cannot be defined, as it is almost

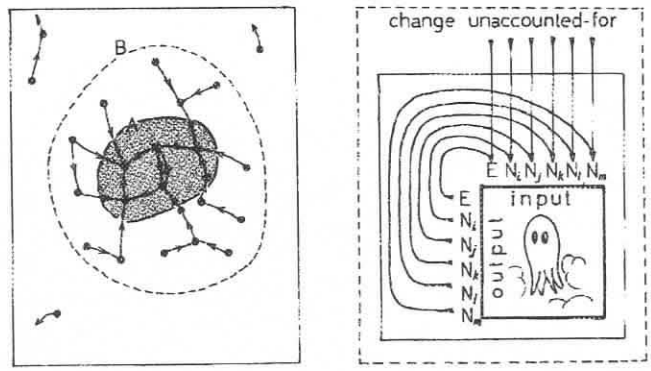


Figure 2. Left: A mapping of stability. States inside the area $A$ are spontaneously interconvertible; if the system is led outside area $A$ but kept inside area $B$, it can regain area $A$. Right: In the small square, a system of equations of the general form $dN_i/dt = e_i N_i + \sum a_{ij} N_i N_j$ has to be imagined. The changes in the values of $N_i$ act as inputs for further changes, and the system eventually attains a steady state. Changes in the magnitudes not accounted for *in* the system represent a test for the stability of the system.

impossible to decide what environmental changes are regular and how far they have affected the evolution of the species present in the ecosystem.

All the facets of the problem of stability of ecosystems are pervaded by history. Nothing is gained by imagining a system subjected to hypothetical changes; the fact is that anything that has passed through a succession or temporal set of selective filters can be called stable, and it can be complex or simple, variable or almost constant. If the capacity to return from a far different state is never needed or realized, the system cannot prove itself stable, but neither is it possible to declare it unstable. Such systems often show a striking stability in taxonomic composition. With this reasoning, the whole notion of stability appears hopelessly confused.

The basic decision is whether one should choose to declare a system stable (a) if it survives many changes but preserves a certain recognizably similar structure (up to what point?), although exchanging species, shifting their proportions, using alternative paths in food nets, and so on, or (b) if it remains much the same and its presumed stability is never tested. Ecologists, myself included, are not categorical about the use of the word stability.[7,8] The same dilemma can be expressed in terms of information: a system may be considered stable because it can continuously pick up information from the environment and process it and change accordingly, or because it has already received or inherited the available and necessary information and nothing new happens for which its organization is not prepared. This second alternative means that the system has attained a degree of homeostasis that makes further changes inconsequential if they fall within the usual range. In a figurative sense perhaps one could speak of extrovert and introvert ecosystems.

In reality the range of possibilities is continuous, extending from the required plastic stability as a condition of survival – extended even to the annihilation of the system? – to the rigid stability permitted only in a constant environment. The ordination along this series could be made using a monotonous function. The wish to retain a qualification (stability) that has a certain tradition is not a real problem –

man hangs on to words even when they are no longer useful. Here we are at a loss to decide whether the word in question should be applied to the head or to the tail of our serpent. Perhaps it would be wiser to refer to the two ends by separate names, for instance, by *adjustment* or *lability* to one, and by *conservatism, endurance,* or *persistence* to the other.

## A PROPOSED MEASURE OF STABILITY (PERSISTENCE)

Any measure has to be based on what is available, assuming that the set of relations linking the elements of the system has passed the proof of time and reflects past interactions between environment and community. A model cannot be made that includes unknown changes in the environment and hypothetical responses of the ecosystem to them. Reasonable approaches have been proposed by Leigh,[9] and Kerner.[10] They are basically similar, since both take as a starting point the general expression of interdependence between species and between species and environment:

$$dN_i/dt = e_i N_i + \sum^{j} a_{ij} N_i N_j$$

where $e_i$ stands for the environment and can be decomposed into a sum of terms relative to different factors, and the $a$'s are positive or negative constants. Thus, the rate of change is made proportional to a linear combination of all possible binary interactions and it is assumed that interaction follows the law of mass action or the probability of encounters.

Leigh[9] relates (conservative) stability to the inverse of the frequency of fluctuations. These can be recognized where the density of species crosses its average value. This model is particularly interesting because stability thus measured appears to be related to other synthetic properties of the ecosystem. Stability is positively correlated with biomass and number of species, and negatively correlated with production.

Kerner[10,11] represents the possible states of an ecosystem as a cloud of probability in a multidimensional space, in which the dimensions stand either for species or for environmental factors. The cloud is denser in the space where the easily interconvertible states are mapped. Kerner characterizes the cloud by a measure which he calls "temperature." High "temperature" means a larger cloud with all possible states more evenly distributed; low "temperature" might be, in consequence, a synonym for conservatism or persistence. One can appreciate the correspondence with the sketch of Figure 2, left, and the pertinence of the concept of "temperature" (if not, perhaps, of the name), which has promising implications for a further application of statistical mechanics to ecology. Kerner's concept is particularly relevant in the sense that it leads to association of maximum stability (persistence, equivalent to low "temperature") with minimum free energy in the system.

Other considerations, not always based on the interactions among species, might also enter into a measure of stability, e.g., the anticipatory power of the system (prevalence of endogenous rhythms over direct responses), the relative importance of negative and positive feedback circuits, the ratio between actual change and possible change (a ratio equal to one would imply no capacity of change when needed), and perhaps the ratio between individual growth and reproduction, related to the size that individuals attain. Important as these considerations may be, they remain far too theoretical.

The need is for a function for what we may name stability, which could be compared with diversity and, together with it, would provide a complete measure of "organization." In my opinion we should follow a criterion analogous to the one that led to the acceptance of Shannon's function for diversity, that is, select a function that gives a fair idea of what is meant, and is practical to compute and resistant to the common hazards of ecological circumstance. As I warned at the beginning, there may be a risk of disposing of the whole concept of stability by sleight of hand, but this I do not believe.

I would propose partitioning the total biomass into species and associating an extinction function with any one of them. If $b_i$ is the fraction that any species ($i$) is of the total biomass so that

$$\sum^{i} b_i = 1 ,$$

and $m$ is the instantaneous mortality rate (or $t$ is the time necessary for the biomass to be reduced to 50%), either of the following expressions of stability or persistence ($S$) will serve:

$$S=(1/c)\sum^{i} b_i/m_i , \qquad S=(1/c')\sum^{i} b_i\, t_i .$$

Some qualities to the credit of these expressions are as follows:

(a) They measure the capacity for storage (of energy, information, etc.) expressed as an average residence time.

(b) The contribution of each species is made directly proportional to the biomass of the species and inversely proportional to its mortality rate. Biomass is a good expression of influence on other species, and mortality reflects the impact of other species or of environmental factors. The average sum of the ratios over the whole system is a measure of the degree of fulfillment of a trend towards homeostasis.

(c) Increase of size of the individuals increases storage capacity, and lengthening of life-span means more independence from time. The species of higher trophic level, having a rather long life-span and a rather high biomass, contribute relatively much to stability and to the value of $S$. Certain elements can contribute to stability not in proportion to their mass, as in the case of resting stages or of unicellular organisms in moments of rapid multiplication and low mortality.

(d) Biomass and mortality are easy to measure, or, at least, less difficult to measure than other parameters. It seems advisable to consider distributions of biomasses rather than of numbers of individuals, but mortality rates can be applied conveniently to the expression selected. I would prefer to speak of attrition of biomass rather than of mortality. Plants are apt to have very different attritions in their different parts: the trunk of a tree contributes more to stability than the green parts; in such cases, perhaps, the $b$'s should be divided further, below the species level. Loss of specimens outside the volume of study, due to other causes, should also be included. Sinking and diffusion, in relation with the turbulence of water, are most important in the definition of $S$ in planktonic communities.

(e) The expressions include an obvious and desirable reference to flow of energy, although only to part of the negative side of the budget (attrition, mortality plus emigration, litter production in trees). With the same primary production, a higher value of $S$ means a slower turnover and, usually, will mean a lesser amount of solar energy necessary for sustaining a given amount of biomass. For every species, $m$

represents the difference between the rate of increase ($r$) and the actual rate of change of the population ($r-m$).

(f) The difficulties posed by the computation of diversity are encountered here also, because the stability or persistence should be estimated from incomplete information, that is, a more or less arbitrary selection from among the species present in the ecosystem. Perhaps some stratified sampling would be advisable, considering the prospective contributions of the different groups of organisms: bacteria, for instance, contribute in a very small amount to stability, because their biomass is low and the rate of change of their populations is high; possibly they contribute more if in a state of suspended metabolism than in activity.

Spectra are necessary in calculating stability (persistence), as well as diversity, and can be prepared with reference to space or to time. What is meant by a spectrum of stability in space is well illustrated by the consideration of plankton communities. If we observe a small space in a geographically fixed position, there is a high probability that within a short time many individual cells will go outside its boundaries: in the frame of our volume of observation extinction is very high. As the size of this volume of observation is enlarged, extinction (in the sense used here), decreases as some power of the size, and it depends also on the turbulence of the water and the motility of the cells. Here we consider the movement of water as a factor in extinction; it is simpler to do so than to follow a vagile population, and is more appropriate also if we want to make comparisons with diversity and other parameters.

A spectrum of stability with reference to time would involve averaging biomasses and mortalities over increasingly longer periods, and computing the function on the different sets of values. In this process small fluctuations in stability may be ironed out. Fluctuations that seem very important may not affect stability very much; for instance, the resting stages make a rather high contribution to stability during the unfavorable season, since, although their mass is not important, their mortality or probability of extinction is also quite small.

## DIVERSITY, STABILITY, AND PRODUCTIVITY

Diversity and stability (persistence), computed as proposed from independent measurements, are complementary, and together, in the suggested form $D-(1/S)$, they describe the actual capacity of the ecosystem as a channel of information at the species level. If stability is very high, diversity is more "valuable."

It has often been assumed that diversity and stability (in the sense of persistence) run more or less parallel. This may be based on empirical evidence afforded by the study of succession, along which it is obvious that there is a correspondence between their magnitudes. Examples supporting this view can be found also in communities not actually linked by relation of succession. For instance, benthic communities are frequently more diverse than planktonic ones and obviously more stable. But I do not see a means of linking the two parameters logically in a simple way, and the frequent positive correlation between them (in the sense accepted here) appears to come from the correlation between the values of $(r-m)$ and $m$. In the discussion that follows, $r$ and $m$ denote, as usual, instantaneous rates of multiplication and of mortality, respectively, but in a sense looser than is customary, that is, applied not to single species, but to groups of species and even to sizable parts of ecosystems.

Together, diversity and stability are expressions of the degree of organization of an ecosystem. All the known data, albeit in a very general form, point to the existence of definite relations between organization and relative "energy flow" in an ecosystem. A convenient measure for purposes of comparison is the primary production divided by the total biomass of the ecosystem ($P/B$); this ratio can be called productivity. This may not be the most frequently used definition of productivity (it is often used as a synonym for production), but I like it because in Latin-derived languages productivity commonly means production in relation to some agent or factor of production.

In any comparison between productivity and organization, if in a first step productivity is compared with one of the components of organization, either diversity or stability, the other one provides a welcome expansion of the scale. Some trivial examples can illustrate this point. In a chemostat with a multispecific population, if flow is accelerated the population can turn unispecific, and at this stage its diversity cannot decrease any more but its stability ($S$) can be further reduced before the population is swept away. A plankton community may attain a diversity of 4.5 bits per individual, and about the same numerical value can be computed in a forest. Yet the forest has a much higher stability, as measured by the proposed standard, and the expression $D-(1/S)$ is much more realistic as a measure of the degree of organization than just $D$, and gives a number that can be compared with the ratio $P/B$ in a more reasonable way.

I have pointed out (Figure 1) that spectra of diversity of plankton may exhibit an excessive diversity at small ranges,[12] as a result of mixing and turbulence; in the same range their stability is extremely low and the expression $D-(1/S)$ is a much more faithful indicator of organization than simple diversity; in short, it normalizes the spectra.

Deep-sea and cave populations are among the systems of lowest energy flow and lowest turnover, yet their diversity is not extremely high, at least among the cave dwellers. But stability is actually very high, and again the expression $D-(1/S)$ appears much more meaningful than just $D$ with regard to general organization and relations with energy flow.

Analogous comments could be made the converse way, that is, when productivity is compared first with stability.

In general, diversity is negatively correlated with productivity, but it is not possible to understand the relation without introducing a dynamic model. Considering the events in a temporal perspective, an increase in productivity means a decrease in diversity, independently of the current numerical relationship between the two quantities. Adequate evidence is found in the study of situations of rapid change, as in plankton cultures or in chemostats. Any sudden increase of the total biomass is unevenly partitioned among the different species, and diversity drops.

It is easy to develop explanatory models. Net rates of increase may be rank correlated with the number of individuals in the set of species, and if they are not, they soon become correlated. Any increase in the total biomass causes the relative abundances of the different species to diverge; another contribution to the expected decline of diversity comes from the species dependent on others, whose response to the initial push given to the mixed population is more or less delayed. In the expression of diversity using factorials, it is simple arithmetic to follow the changes step by step, each step consisting in the addition or separation of one individual, or in the substi-

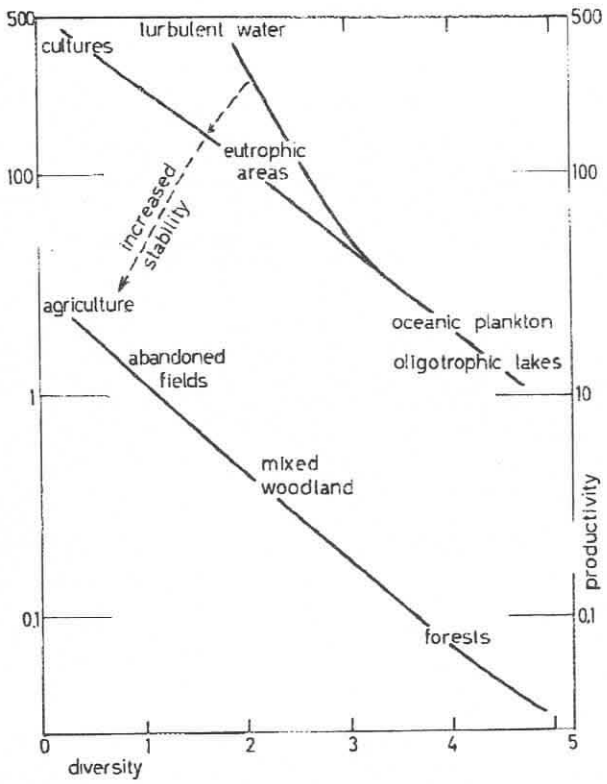


Figure 3. Approximate relations between productivity (yearly primary production per total biomass) and diversity in a number of typical ecosystems. The scale of productivity has been interrupted diagonally. The concept of stability, in the sense of persistence, is convenient for simplifying representations like this one.

tution of one individual of one species by one of another; the substitution of an individual of a rarer species by one of a commoner species decreases diversity, and vice versa.

The comparison between diversity and productivity in different sorts of ecosystems (Figure 3) not only serves to illustrate the general form of the mathematical function to be expected in the relation between diversity and productivity, but also is interesting in terms of the definition and nomenclature of stability. At one end (at left in Figure 3) great changes in productivity are associated with quite small changes in diversity; diversity is always rather low and this is the domain of adjustable stability, or low stability in the terminology used here. At the other end (at right in Figure 3) small changes in productivity are linked with considerable changes in diversity, and this is the area of conservatism, persistence, or "true" stability. The general pattern of relations suggests a semilogarithmic function, and moreover it is clear that something else – and that is stability – has to be included in the model to bring in to a line the different kinds of ecosystems.

We arrive at the same sort of semilogarithmic relation by following another way. Elsewhere[12] I tentatively related the second derivative, with respect to time, of biomass with the first derivative, also with respect to time, of diversity, but I was not

satisfied with the result. Nevertheless a model more or less like this one should contain some truth. In a system in equilibrium (in every species $r-m=0$, and in the whole system total respiration amounts to the gross primary production) diversity keeps increasing to an upper limit; it is some excess of $r$ over $m$ in any group of species that reduces diversity, and it seems that if $r-m$ is constant for a while, diversity is stabilized at a lower level, and if $r-m$ keeps increasing, diversity drops continuously and eventually becomes zero. There is nothing wrong in stating the same arguments with reference to the whole ecosystem, and in terms of gross primary production and total respiration. So far as primary production keeps increasing, and if it increasingly outdistances respiration, diversity is expected to drop.

These statements can be summarized by writing tentatively

$$D=K-\frac{dB/dt}{B}, \qquad D=K-\ln\left(\frac{P}{B}+1\right)+M$$

where $K$ is a constant, $D$ is diversity, $B$ is biomass, and it is accepted that $dB/dt=r'B-MB$ and $P/B=e^{r'}-1$; $P$ stands for primary production and $M$ represents a rate of loss of total biomass. This formulation is not very rigorous, but probably apt to express the kind of relations among different parameters of the ecosystem. Some inconsistency in the use of $r'$ disappears if one writes $P/B=e^{r'}-C$ with an auxiliary constant $C$, related to the maintenance energy and probably characteristic of whole classes of ecosystems.

The changes in diversity so far discussed do not necessarily imply changes in stability. Stability can be introduced into this expression if we remember that $1/S$ is somewhat a measure of $M$, the necessary adjustment being done in the $c$ of

$$S=\frac{1}{c}\sum^{i} b_i t_i .$$

In consequence we are led to write

$$D-\frac{1}{S}+\ln\left(\frac{P}{B}+1\right)=K$$

where, in the maximal degree of maturity, $S\to\infty$, $P/B\to 0$, and $D\to K$, so that $K$ appears as an upper limit to diversity.

It may be desirable to decompose $P/B$ into the form

$$P/B=(P/R)\cdot(R/B)$$

where $R$ stands for respiration, and this leads to

$$D-\frac{1}{S}+\ln\frac{P}{R}+\ln\left(\frac{R}{B}+\frac{R}{P}\right)=K \qquad (1)$$

where often $\ln(P/R)$ will be zero.

This expression is consistent with many empirical relations, but it is not without its difficulties. Essentially it embodies nothing new, but it relates four parameters ($P$, $B$, $D$, $S$) of paramount significance in ecology. As all of them are measurable independently, the expression can be tested. In a general way (Figure 3) it seems appropriate. Here it is proposed tentatively only as a starting point for discussion. Further empirical evidence may help to improve it or may favor its total rejection.

If acceptable, it may be useful for prediction and for the indirect estimation of some of the essential parameters.

The expression proposed embodies my opinion that the relations between diversity and stability are based on the fact that species with a higher turnover react more quickly to environmental change; in other words, they are based on the correlation, usually positive, between $(r-m)$ and $m$, in species as well as in ecosystems. This is if we consider short periods of time; over indefinite lengths of time the positive correlation is between the variance of $(r-m)$ and the average value of $m$.

## THE STUDY OF ORGANIZATION IN SPACE

Any expression of the sort proposed will remain inoperative if it is not able to encompass the fact that ecosystems are spatial structures as well as temporal ones. Knowledge of spatial gradients on the different magnitudes are essential to the understanding of the structure and workings of ecosystems.

Different approaches are possible. One of them is to develop expressions using (partial) derivatives with respect to one $(x)$ or more dimensions of space, as, for instance,

$$-\frac{dD}{dx}=\frac{dB}{dt}\cdot\frac{dB}{dx}.$$

This expression states that, according to whether the value of $dB/dt$ is greater or less than zero, gradients in diversity and in biomass may be parallel or opposed. If biomass decreases, when production is insufficient to conserve the equilibrium, the gradient of diversity is expected to run parallel to the gradient of biomass; but if biomass is increasing, the gradient of diversity is opposed to the gradient of biomass. Such relations are substantiated by the comparison of transects in the margin of fertilized and unfertilized fields, and they are also clear in patches of plankton.

Another approach, which has the advantage of being very general, consists of applying the general expression (1) to local segments of an ecosystem and then making comparisons. Suppose that productivity is uniform over a wide area. This means that $K-\ln[(P/B)+1]$ is made constant everywhere, but diversity and stability may fluctuate in small spots $(i, j)$. We have

$$D_i-\frac{1}{S_i}=K-\ln\left(\frac{P}{B}+1\right), \qquad D_j-\frac{1}{S_j}=K-\ln\left(\frac{P}{B}+1\right),$$

$$D_i-\frac{1}{S_i}=D_j-\frac{1}{S_j}, \qquad \frac{D_i-D_j}{S_j-S_i}=\frac{1}{S_iS_j}.$$

This implies that local differences in diversity are opposed to differences in stability, their ratios being dependent on stability. Under conditions of rather low stability more important local differences in diversity are to be expected.

If the comparison is made not between nonoverlapping and equal areas $i$, $j$, but between small areas $i$, and larger areas including the former, $k$, some modifications must be introduced because in small areas the constant $K$ may have a smaller value, $K_i+C=K_k$, and the expression becomes

$$\frac{C+D_i-D_k}{S_k-S_i}=\frac{1}{S_iS_k}.$$

This may be a starting point for discussion of some properties of spectra.

If the two compared systems have different productivities, the more productive one, having a larger ratio $P/B$, should be less diverse or less stable or, possibly, both, than the other. If the two systems are coupled and have inverse values of $P/R$, often the autotrophic will be less diverse and/or less stable than the heterotrophic (e.g., dystróphic lakes); but if the ratio $R/B$ is very high in the heterotrophic one, as is frequent (polluted water), the heterotrophic will be less diverse or less stable.

In general, the expressions deduced from the general one seem to be adequate to describe the behavior of ecosystems, and for this reason it is assumed that the general expression is basically sound.

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## DISCUSSION

JOHANNINGSMEIER: How are $D$ and $S$ measured, in what units?

MARGALEF: $D$ is measured in bits per element, usually in bits per individual. $S$ is measured in half-life or in the inverse of mortality rate, and in both cases its dimension is $T^{-1}$. But, of course, if a definite meaning is given to the $c'$ in

$$\frac{1}{c'}\sum^{i} b_i t_i\,,$$

as, for instance, a fixed value of turnover, then $S$ has no dimension. It may be a matter of choice in order to get numerical and dimensional consistency in the expressions. I am interested here only in the general structure of the relations. Total consistency is not necessary to get an idea of what $K$ means, because if persistence goes to infinity, its inverse goes to zero.